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Philosophy and evolution

Comments on Michael Ruse: Karl Popper's Philosophy of Biology*

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ABSTRACT: Karl Popper has at many occasion shown an interest in the problem of biological evolution. Although believing in neo-Darwinism he is unbiased enough to see that from a philosophical point of view the theory has indeed some serious shortcomings. Michael Ruse, an ardent neo-Darwinian has, in the article discussed here, tried to show how it is possible to overcome the difficulties observed by Popper.
In the present author's opinion Ruse has not been very successful in this endeavor, for Popper's observations imply, in fact, the falsification of the neo-Darwinian micromutation theory. On the contrary if we adopt the macromutation theory it is found that not only does it allow for the resolution of all the problems which worried Popper, but it furthermore corresponds exactly to the model for the growth ***and*** *evolution of human knowledge advanced by Popper.*

Karl Popper and Michael Ruse are both avowed supporters of the currently prevailing theory of evolution which passes under the name of 'neo-Darwinism'. In spite of this fact their evaluations of the status of the theory differ considerably. Thus, whereas RUSE (1973; 1977a; 1977b), considers that the theory is almost on par with other scientific theories, POPPER (1973, 1976) has declared that

> Darwinism is not a testable scientific theory but a metaphysical research programme a possible framework for testable scientific theories (1976, p. 168).

The divergent positions adopted by the two savants, outsiders as far as biology is concerned, and specialists with regard to philosophy, are of considerable interest to persons interested in the philosophy of biology.
The present essay is written primarily as comments to the paper in which

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RUSE (1977a) discusses Popper's philosophy of biology. However, since my views on the mechanism of evolution differ fundamentally from those inherent in the neo-Darwinian theory, I shall begin by presenting the stand upon which my comments are based. After a comparison of the viewpoints of Popper and Ruse I shall go on to show that Popper's notion on the growth of human knowledge actually coincides with that of the theory of progressive evolution, in my interpretation the only surviving part of Darwinism.

1. THE THEORIES ON THE MECHANISM OF EVOLUTION

It is a common view that one single theory is enough to account for all aspects of evolution, namely, neo-Darwinism. As I have shown elsewhere (Løvtrup, 1982, 1987a), we need at least four theories for this purpose, the theory on the reality of evolution, the theory on the history of evolution, and two theories on the mechanism of evolution. The first of the latter, the epigenetic theory, deals with the *creation* of living organisms and the second, the ecological theory, with their *survival*. The theories on the reality and the history of evolution are creations of Lamarck, who also submitted a theory on the mechanism of evolution, which has suffered a changing fate in the course of time; thus, after having been neglected or rejected since its publication it became very popular towards the end of the last century. Subsequently it was disowned during most of this century, but recently it has experienced a certain renaissance (cf. HO and SAUNDERS, 1984).

Darwin's aim was to explain the mechanism of evolution, and it is generally assumed that he contributed to the aspect of evolution represented by both of the mentioned theories. The epigenetic theory refers to happenings occurring inside living organisms. Living beings arise during ontogenesis, a process which stretches from fertilization to death. However, the most important creative events take place during the earliest stages of ontogenesis, during embryogenesis (LØVTRUP, 1974; 1986a; 1986b). Without a thorough insight in embryology it is impossible to form a valid conception about the way living organisms come into existence. However, although embryology is briefly discussed in *On the Origin of Species*, Darwin did not contribute to the epigenetic theory. Rather, like Lamarck before him, he expounded a micromutation theory, asserting that all major changes occurring during evolution are the re-

sult of the accumulation of slight individual variations. According to Darwin the latter are inherently random, but their purposeful accumulation is ensured by natural selection.

This notion was heavily criticized as soon as it was published, not only by Darwin's critics, but also by some of his supporters and friends (LØVTRUP, 1987a). This criticism was based on the fact that the theory predicts that each step in the accumulation of such small variations must be useful in order to be preserved. Several of Darwin's opponents, for instance Mivart and Kölliker, pointed out that many of the transitions, which must have occurred if evolution has taken place, were such that the intermediate stages could not possibly have been useful. Von Baer, the outstanding embryologist, argued that the most important evolutionary modifications must involve changes in the early stages of development, and that considerable changes in the adult phenotype may follow from rather slight changes at this point. Apart from those theoretical objections there were some practical ones. Thus, if Darwin's theory were right, then the breeding of plants and animals would not only require superhuman foresight, but also enormous lengths of time. In fact, both before and after Darwin, practical experience has shown that sudden variations, with effects well beyond that implied by Darwin's micromutations, may be preserved simply through inbreeding.

In the course of time many theoretical considerations and empirical observations have been found to contradict the mucromutation theory (REID, 1985; LØVTRUP, 1987b) If this is all there is to Darwin's theory then, rather than claiming it to be untestable or unfalsifiable, it would be more correct to accept that it has been falsified. But in fact, Darwin's theory deals also, and primarily, with phenomena taking place at the ecological level or organization. It was indeed a rash step to extrapolate from one level to the other, to claim that natural selection, an ecological phenomenon, can affect the epigenetic process through which living organisms are created. Nevertheless, I believe that very few of Darwin's opponents have ever denied that natural selection is involved in evolution. Yet, if it cannot create evolutionary innovations, as suggested by Darwin, what can it do?

2. SURVIVAL, SELECTION AND ISOLATION

It is my opinion , one which I share with many biologists in the past, and some in the present, that what natural selection can do is to ensure that evolution is progressive, giving rise in the course of time to living beings

with ever increasing complexity of organization. In achieving this, natural selection functions as a Maxwell's demon; whenever comparison is allowed for, that is, whenever competition obtains between different forms, natural selection ensures the survival of the progressive or dominant form. This, I contend, is an evolutionary law, based on a mechanism of natural selection which, being interspecific, coincides in part with the one envisaged by Darwin, if not by his present-day successors. This law does not predict the course of future evolution, but it makes predictions about observations concerning the history of the unique process of evolution which has occurred during perhaps the last three billion years. These predictions may be tested in two ways, directly and indirectly. The first consists in studying the remains of life in the past, as they are preserved in the fossil record. However incomplete the latter may be, it seems to testify that evolution has proceeded towards higher forms of life. The indirect method is based on the phylogenetic classification of living forms, and again it can hardly be questioned that the picture reflected there demonstrates that evolution has been progressive (LØVTRUP, 1987a).

This conclusion was arrived at by Lamarck when he first submitted the idea of phylogenetic classification. Unfortunately, in the footsteps of the master, it has been refuted by many Darwinians. However, I believe it is generally accepted that life began at a stage well below the present archaebacteria and that – in the main phylogenetic lineage – the latest productions are the warmblooded animals, birds and mammals. On this background it is to me completely incomprehensible that anybody can deny that the evolution has been progressive.

As far as survival is concerned, Darwin's theory is incomplete, for organisms may also survive in isolation, a phenomenon which may be either random or nonrandom (LØVTRUP, 1977; 1982; 1987a). Isolation plays an important role in current evolutionary theory, not the least through the influence of MAYR (1942; 1982). But the function ascribed to isolation is to allow for 'speciation', that is, divergent evolution. It is seldom empha-sized that isolation also involves a chance for survival exempt from competition with dominant forms , thus in the absence of natural selection. It is therefore a mistake to refer survival to one single property, fitness, as is commonly done. Rather, survival may ensue from three different causes, dominance, cunning or luck. In the first case selection is the exe-cutive agent , in the two last ones it is isolation. Darwin produced two falsifiable theories, one concerning the way evolutionary innovations are created through the accumulation of micromuta-

tions, and one concerning the influence of natural selection on the direction of evolution. As we have seen, the first is falsified and the second borne out, but it is incomplete as regards the question of survival , and its outcome differs from that envisaged by Darwin.

3. ON THE PREDICTION OF EVOLUTION

RUSE (1977a) begins with a reference to *The Poverty of Historicism*, in which Popper claims that

> there can be no prediction of the course of human history by scientific or any other rational methods (p . 639),

a view which may be generalized, I believe, to state that we cannot predict the future. This may seem to be in conflict with the aim of science which, according to Popper, is to deduce the consequences of some particular statement (theory or law), and to test its validity by investigating whether matters in the real world correspond to the predictions. In a certain sense it cannot be denied that under these particular circumstances scientists are indeed predicting the future, and yet, I believe that it would be closer to reality if it was claimed that what is predicted is not the future as such, but only future scientific observations. It is enough to think of volcano eruptions and hurricanes to realize that even in physical sciences like geology and meteorology our powers of predicting the future are very limited. This holds even for man-made products; no bridge would ever collapse if engineers could predict the future. I believe this distinction is very important, because it implies that the outcome of events which took place in the past , if unrecorded so far , may be used to test scientific theories. This is an approach which is applied in both geology and cosmology, and it is of particular importance in biology, especially for the study of evolution. For it is evident that the aim of evolutionary theory is not to predict future evolution , but rather to account for – to explain – the way that life has evolved on our planet.

Thus , if 'laws of evolution' are understood to predict the course of future evolution, then we must accept Popper's claim that there are neither laws of succession, nor laws of evolution (RUSE, p . 639).

But Popper further asserts that the reason for this state of affairs is that

> the evolution of life on earth, or of human society, is a unique historical process (RUSE, P. 639).

This is of course true, but there is a fundamental difference between the two processes mentioned by Popper. Thus, whereas history deals with single events that are never repeated, evolution is concerned with the acquisition of inheritable properties, which are reproduced again and again during the ontogenesis of the descendants of the organisms in which a certain property first arose. This circumstance implies that evolutionists have a chance to test their predictions in a way that is unknown in the historical sciences. An overwhelming part of the past events which were involved in evolution will forever be unknown to us, but if we have more modest ambitions, say, if we just want to know the course or history of evolution , and if we confine ourselves to organisms living today, then we may still be able to establish some evolutionary 'laws'.

The way towards this goal goes through phylogenetic classification, based on an analysis of the distribution of characters in the various taxa of living organisms. I shall not here discuss the method employed for this purpose except to point out that it is probabilistic, being founded on the assumption that if, between three taxa, one pair has more characters in common than any of the other two possible pairs, then this pair of taxa is presumed to have a more recent common ancestry than any of the other ones.

In this way we can establish a theory dealing with the course of evolution without any assumptions about the mechanism through which this process was accomplished. As far as this point is concerned Popper claims that such a process [*as the evolution of life on earth*], we may assume, proceeds in accordance with all kinds of causal laws, for example, the laws of mechanics, of heredity and segregation, of natural selection, etc. (RUSE, p . 640). This we must admit, even if a biologist is here missing some very important biological laws, those, for instance, which control cell division, cell differentiation and the various dynamic events which are responsible for morphogenesis and growth during the ontogenesis of plants and animals. For to the extent that the phyletic succession of adults is the product of successive ontogenies (GARSTANG, 1922, p. 48),

it follows that if we want to know the laws concerning the epigenetic aspects of evolution, the point missed by Darwin, then we must study just these processes. This may to a large extent be done on the basis of von Baer's work, and since the processes in question are reproducible events, nothing prevents that the laws ruling at this level of organization eventually become established.

Ruse interprets Popper's view to imply that he denies

> extrapolations pointing to a general progression in the course of evolutionary history,

and thinks that

> the great majority of evolutionists would no doubt join with Popper (p. 640).

And the reason for this is that evolution may at times be 'degenerative', involving losses of various kinds. But this argument loses value if we accept that there are two kinds of evolution, divergent and progressive, respectively, for all observations support the notion that degenerative evolution occurs in isolation.

Ruse next mentions the so-called evolutionary 'rules' and 'laws', like 'Cope's Rule' and 'Dollo's Law', observing that they have,

> an awful lot of exceptions... Popper points out that... trends are not laws. A statement asserting the existence of a trend is existential, not universal (p . 641).

But this is not the point! In biology there are no universal laws, only probabilistic ones (LØVTRUP, 1987b). And if, as quoted by Ruse, a certain law has 36 % exceptions, then, I guess, it may still be accepted as a valid probabilistic statement.

Ruse next turns to the claim made by Popper about Darwinism being a metaphysical research programme, which was quoted in the introduction of this essay. Like so many others, Popper apparently bases his criticism on Spencer's maxim 'the survival of the fittest'. I agree that this is not much more than a tautology, but I do not think it is a fair point of departure for the evaluation of Darwinism. In fact, in agreement with statements by Popper quoted later, the theory does in fact make testable, and *falsified* predictions, but unfortunately this is not generally accepted by adherents to the theory.

Popper has tried to test the theory by attempting to see what it might predict about conditions on Mars (RUSE, p. 643). In my opinion Darwinism is a theory dealing with the situation prevailing on our own planet, and therefore it is a great mistake to make such a *Gedankenexperiment*; we happen to know that the laws of physics and some of chemistry are valid in the universe, but we have no reason to presume that the biological laws known to us are also valid there.

4. ADAPTATION AN ELUSIVE CONCEPT

The next topic addressed by Popper is 'adaptation'. To every observer of nature living organisms are wonderfully 'adapted' to live in the particular environment in which they happen to live. Thus some plants live in the desert, and some submerged in water, some animals spend an essential part of their lives in the air, others live beneath the surface of the earth without any exposure to the daylight; examples of this kind are infinite. To a believer in Darwinism it is quite natural to assume that this 'adaptation' has been accomplished through natural selection. For those who are accustomed to repeat uncritically ideas submitted by others, this may sound quite plausible, but in fact, a little of the critical attitude, so much praised by Popper, suffices to show that 'adaptation' is a rather obscure phenomenon. Woodger asserted:

> Organisms are adapted to their environments. And all that this means is that their characterization is such that in those environments they are able to live (1929, p. 436)

This is just the point! We are unable to imagine an organism subsisting in an environment to which it is not adapted, and if living beings are by necessity adapted to their particular milieu, then it is difficult to see how natural selection can be made responsible for the variation in adapta- tion implied by the theory of evolution. One might of course suggest that selection improves the adaptation, but how could that be measured ? If each organism is adapted to its particular environment, a comparison is impossible. Like Woodger, Popper realizes the weakness of this concept:

> Take 'Adaptation'. At first sight natural selection appears to explain it, and in a way it does, but it is hardly a scientific way. To say that a species now living is adapted to its environment is, in fact, almost tautological. Indeed we use the

> terms 'adaptation' and 'selection' in such a way that we can say that, if the species were not adapted, it would have been eliminated by natural selection. Similarly, if a species has been eliminated it must have been ill adapted to the conditions (RUSE, P. 646).

The interpretation given here undoubtedly would be accepted by many neo-Darwinians. And yet, if we consider the causes which may lead to extinction, it seems necessary to accept two possibilities: catastrophes and competition. The attitude towards the possible occurrence of catastrophes during the history of the earth has changed considerably; in the early decades of the last century the catastrophe theory was commonly accepted, but owing to the influence of Lyell it has been in disrepute for a very long time. It seems, however, that recently a more positive attitude has prevailed (cf. RAUP, 1984). Yet, if catastrophes have occurred, and if they have led to extinction, then this cannot be referred to lack of adaptation, for clearly it is impossible to be adapted to catastrophes, at least in the way adaptation is understood by the neo-Darwinians.

On the other hand, extinction may also be the outcome of competitive selection. Selection may be either intraspecific or interspecific. The former may in principle lead to change, to further adaptation, but not to extinction. Interspecific selection may lead to extinction through competition, but at the cost of the plausibility of adaptation. For if one organism is adapted to a particular environment, then it ought to be protected against transgressions by members of any other less adapted taxon. If this prediction is falsified, and natural history testifies to the fact that it has happened repeatedly, can we then say that the successful invaders were better adapted than the natives? Does not this statement deprive the notion of 'adaptation' of all sense? In my view this problem can be solved only by introducing the concept of 'dominance', which does not correspond to adaptation, but well to adaptability, as pointed out by WOODGER (1929) and HUXLEY (1942).

But, as shown by Popper, instead another road is taken:

> Adaptation or fitness is defined by modern evolutionists as survival value, and can be measured by actual success in survival: there is hardly any possibility of testing a theory as feeble as this (RUSE, p. 646).

Here we observe one of the illusory tricks of neo-Darwinism: the theory is wholly based on adaptation, but since this cannot be measured, one

chooses instead, under the influence of Spencer's maxim, fitness as a measure of evolutionary success. But how are we then to measure fitness? The fundamental idea is that natural selection will ensure differential reproduction; the more fit will produce more offspring than the less fit. If we base our reasoning on the Darwin–Wallace Malthusian axiom that the environment is satiated at any moment, then it follows that on the average every fertile individual will contribute one fertile offspring to the following generation, independently of the number of offspring hatched or born. The relative fitness of two populations or taxa might therefore be evaluated after surveying the fate of a whole generation under natural conditions. Another alternative would be to compare the changes in number of two populations during several generations, but as already pointed out, this would measure dominance rather than fitness–adaptation.
If the present reasoning is correct it thus follows

> (I) that extinction is impossible, except if we allow for catastrophes or interspecific competition, and (II) that adaptation –or fitness– cannot be objectively measured.

This seems to be a serious challenge to the neo-Darwinian theory. Nevertheless, Ruse is not perturbed:

> certainly the differential reproduction makes evolutionary theory testable. If we all just budded off one and only one offspring asexually, evolutionary theory would be false (p. 647).

I fail to see that. For one thing, even asexual organisms have undergone evolution. Furthermore, one and only one offspring is a rather strict requirement, because most organisms take part in biological cycles involving that they perish before reaching maturity . If we allow for this and assume that survival is fortuitous, then we reach a contradiction of the theory advocated by Ruse. In fact, I believe Popper is right, it is very difficult, even impossible to test the neo-Darwinian theory on this point. It seems that, as is often the case with the examples used by philosophers of science to illustrate their views, the one proposed by Ruse as an attempt to test the theory is not particularly convincing. Another one is the following:

> winglessness seems to be of value to insects and other small animals on oceanic islands (because they stand less chance of being blown away) (p. 648).

I shall not discuss whether this argument, dealt with already by Darwin, is really convincing, but it should not be forgotten that it is quite common that even birds on isolated islands have lost their wings. In this case the notion about being blown away is much less credible. Since it would be of great advantage to evolutionary theory if an explanation could be found, common to both insects and birds, I suggest the interpretation that qualities, which otherwise are important for survival, may be lost with impunity in isolation, such as it may obtain, for instance, on oceanic islands.

In this context Ruse also mentions 'industrial melanism', the phenomenon that moths in several cases have changed colour because the trees upon which they settle have become darker owing to pollution. This is not a very good example from a Darwinian point of view, because it does not occur through accumulation of micromutations; it may therefore support the notion of natural selection, without corroborating the micromutation theory. However, it seems that even the selection aspect is much less clear-cut than formerly believed (MANI, 1980; SERMONTI and CATASTINI, 1984; LAMBERT, MILLAR and HUGHES, 1986).

We may mention two other cases, one referred to by Ruse, one by Popper. The first is sickle-cell anaemia, the second penicillin-resistant bacteria. In both cases se-lection of a single mutation, clearly a macromutation, is involved. These three cases strongly support the importance of selection for survival, but they do not show

(1) that a gradual accumulation of mutations is possible or

(2) that this agent can accomplish taxonic evolution.

As an argument against Popper Ruse now mentions genetic drift, the mechanism proposed by WRIGHT (1931) to allow for the survival of neutral or even deleterious mutations. This seems to be a rather ill-advised argument, for genetic drift is based on fortuitous events; by this expedient evolution becomes unpredictable, a situation which corresponds to the stand taken by Popper.

5. THE REFUTATION OF GRADUAL EVOLUTION

Popper subsequently deals with the gradualness of evolution, i.e., the micromutation theory:

> Gradualness is thus, from a logical point of view, the central prediction of the theory. (It seems to me that it is its only prediction). Moreover, as long as changes in the genetic base of the living forms are gradual, they are –at least 'in principle'– explained by the theory: for the theory does not predict the occurrence of small changes, each due to mutation (RUSE, p. 649).

Popper goes on to emphasize that this predictability amounts to very little, personally I believe that at most it may allow for predicting future observations under strictly experimental conditions . It is surely impossible to make any predictions whatsoever about events taking place under natural conditions.

The point of gradualness, that is, the phenomenon implied by the micromutation theory, is one of the most obscure aspects of the Darwinian theory. For as mentioned already, the evidence, theoretical as well as practical, speaks so heavily against it. This was known to Darwin, and, in spite of all endeavours during more than a century, no convincing examples demonstrating that the accumulation of micromutations can be of *evolutionary* importance have ever been observed. This does not mean that accumulation of mutations of slight effect is impossible, but there is no evidence that it could ever lead to the formation of new species.

So it is not at all surprising that Popper is skeptical about the gradualness, and regrettable that he did not arrive at the conclusion that this aspect of Darwinism is false. But Popper goes on making a statement which apparently is shocking to Ruse:

> It is clear that a sufficient increase in fecundity depending fundamentally on genetical factors, or shortening of the period of immaturity, may have the same survival value as, or even a greater survival value than, say, an increase in skill or intelligence. From this point of view it may be a little hard to understand why natural selection should have produced anything beyond a general increase in rates of reproduction, and the elimination of all but the most fertile breeds (RUSE, p. 651).

The idea stated here may be put a little more bluntly by claiming that if the goal of evolution is adaptation, and if adaptation equals fitness, and fitness success of reproduction, then evolution should never have exceeded the prokaryote level, for the fecundity obtaining there has at no time been surpassed at the higher levels. Thus, once more we come to the conclusion that evolution as adaptation is a *cul-de-sac*, we must have another kind of evolution, upwards as it were

before we can really account for the testimony of our own senses.
In passing it may also be mentioned that it would seem counterintuitive to presume that natural selection should ever have been able to drive evolution towards the higher levels of organization where, in general, the number of offspring is smaller than at the lower levels. Surely, natural selection has much less material to work on among the higher animals than in the world of bacteria. In this context Ruse quotes a very interesting example:

> It has been argued by David Lack simply that there is selection of the individual plover for such a [stable] clutch size more eggs and the individuals collectively are less fit, and a fewer egg number does not make for fitness which compensates for the fewness in number... Incidentally, there is nothing unfalsifiable about the evolutionists' position here that whatever the reproduction rates may be evolutionary theory will necessarily have an answer. If experiments showed (what they do not) that plovers given additional eggs have more fit offspring, then Lack would be wrong (p. 651).

I am not sure that I know of the experiments referred to, but I am sure that in isolation –for instance under experimental conditions– plovers given additional eggs would have a larger progeny, which in turn might have a larger progeny, etc. In fact, the same might happen in nature if some organisms were isolated in an empty niche. The fundamental premise in the selection theory is satiation of the environment; if this condition is not fulfilled, then not only Lack, but even Darwin would be wrong.

6. POPPER'S REVISION OF THE THEORY OF EVOLUTION

Owing to Popper's dissatisfaction with the present state of the Darwinian theory he has proposed to 'enrich' it by introducing a set of new genes which are meant to ensure directed rather than random evolutionary changes. Thus it is postulated that besides '*a*-genes', which control the final anatomy or morphology required by the adaptive change, there are also '*p*-genes' which control preferences and '*s*-genes' controlling skills. Popper thus envisages that these genes function in the succession "*psa*", that is, an organism first experiences a preference for a new way of life, as this is adopted the necessary skill is acquired, and finally the body is transformed to fit the needs. I want to make the following comments to this theory:

(1) It may be an enrichment, but above all a complication. According to the micromutation theory every major change requires the accumulation of a large amount of mutations. This means that enormous lengths of time are required to accomplish evolutionary changes, a circumstance which has been a burden, an insuperable one, I believe, on the theory of evolution. But surely, Popper's suggestion only increases this burden.

(2) A new theory is hardly needed to impose direction on evolutionary advance; if natural selection cannot accomplish this, then the theory fails.

(3) In fact, what Popper evidently tries to do, is to introduce a mechanism of 'preadaptation'.

There are many evolutionists who have felt the necessity of some kind of preadaptation, for how can the members of some taxon, adapted to a particular form of life, suddenly leave their station and adopt a new life style without possessing at the outset the adaptations required? One possibility is that a few individuals are fortuitously isolated in a new environment, and simply are forced to adapt to it in order to survive. I believe that this notion lies behind Mayr's concept of 'allopatric speciation' (1942), and it is also implied by the theory of punctuated equilibria by ELDREDGE and GOULD (1972). As long we are dealing with minor changes this solution may be acceptable, at least from a theoretical point of view, but it needs very little imagination to envisage that many of the changes which have occurred during evolution must have been so radical that this explanation fails. In fact, the only theory which can account for such 'revolutions' is the macromutation theory.
As it turns out, inspired by the work of MACBETH (1971), Popper has himself played with the idea of macromutations, that is, Goldschmith's 'hopeful monsters'. Regrettably, he suggests that the macromutations may concern behaviour rather than morphology. The macromutation theory was discussed by Ruse who produced the classical objection:

> To take but one point –– is this monster supposed to be of a species different from its parent? If it is not, then Popper is ignoring the major evolutionary problem of speciation. If it is... then with whom is it going to reproduce, since its parents' species is ruled out? (RUSE, pp. 656-657).

Unwittingly Ruse is here creating confusion because he fails to discriminate between convention and logical reasoning. The concept of 'species' is a convention. From an evolutionary point of view a new species exists when members of some species have become sexually isolated from the remaining members. From a taxonomic point of view a new species may have arisen

when a significant phenotypic difference has been established. The mutations responsible for these two kinds of change are independent (MAYR, 1982).
Mutations leading to sexual isolation often involve modification of the genotype. If such changes occur in a single individual, then the situation proposed by Ruse prevails, that is, the organism cannot reproduce. But if the change takes place in the germ line, a whole clutch may carry the mutation , and its survival therefore meets with no obstacles . If, on the other hand, the mutation affects only the phenotype, then it may be fixed through inbreeding without further ado. This is the way many odd forms of domesticated plants and animals have survived. Ruse, the lover of dogs, ought to know that.

7. PROGRESS IN EVOLUTION AND IN HUMAN KNOWLEDGE

According to POPPER (1973) progress in human knowledge may schematically be represented in the following way:

$$P_1 \rightarrow TT \rightarrow EE \rightarrow P_2$$

where *P* stands for 'problem', *TT* for 'tentative theory' and *EE* for 'error elimination'. Popper has repeatedly stressed that the last step corresponds to natural selection , and that consequently there is an analogy between evolution and the advancement of human knowledge. The remarkable feature of this programme is that although every solution of a problem leads to a new one, it nevertheless leads to progress, an old theory is rejected only when a new, more comprehensive and more bold one, has been invented.
If this is true, and personally I am convinced that it is, then logical reasoning would lead to the conclusion that natural selection must be responsible for the undisputable fact that evolution has been 'progressive'. The reason why so many have objected to this conclusion is that it is just as indisputable that it has not 'always' been progressive. However, the solution to this problem is implied by Lamarck's notion that there are two kinds of evolution, divergent (adaptive) and progressive. Typical of divergent evolution is that it takes place in isolation, that is, in the absence of natural selection, a circumstance which may permit the survival of regressive alterations.

Thus, there are no valid logical objections against the notion that progressive evolution has taken place, and the only agent enabled to accomplish this is natural selection. Natural selection is thus completely analogous to Popper's error elimination; as the latter leads to better theories, the former leads to more and more dominant organisms.

The question remains: what corresponds to Popper's tentative theories? On this point Ruse comes with a very noticeable comment:

> But the fact of the matter is that tentative knowledge solutions are frequently fairly large (saltationary) (RUSE, p. 659).

Indeed, reading Popper it cannot be doubted that the advance in knowledge — for instance, Ptolemaeus, Copernicus, Kepler, Newton, Einstein — is characterized by intellectual giants who revolutionize science, while in the intervals between these contributions scientists are engaged in modifying and applying the theories in question. In this respect I think we must accept Kuhn's distinction between 'paradigm shifts' and 'normal science' (1962).

In my view Popper's own work ought to have convinced him that if the analogy between evolution and advance in knowledge is to be complete, then he should have embraced the macromutation theory. It would not be difficult to demonstrate that the analogy is exhaustive in so far as even in the field of knowledge obsolete theories may survive in isolation; Popper has himself pointed to such phenomena as psychoanalysis, Marxism, and astrology (1972).

8. CONCLUSION

I have here attempted to analyze the criticism which Ruse, a well-known adherent to neo-Darwinism, has raised against Popper , who also claims his belief in the value of this doctrine , even if he questions its validity as a scientific theory. Thus, on the basis of the two fundamental tenets of neo-Darwinism, micromutations and natural selection, Popper comes to the conclusion that in many ways the available empirical evidence does not correspond to the predictions that may derived from the theory. One reason for these different attitudes is clearly that Ruse is much better acquainted than Popper with the literature on Mendelian population ge-

netics, which he frequently quotes , perhaps less critically perhaps less critically than might be expected.

At several occasions (LØVTRUP, 1977; 1982; 1987a) I have shown that the currently accepted theory has two weaknesses. The first is that it is a micromutation theory. Ever since Darwin published his theory, quite a few of his opponents have asserted that many of the changes which occurred during evolution cannot have been the outcome of mutations with slight effects. In support of the opposing claim that the involvement of macromutations is more than pure speculation, it has often been pointed out that the breeders of animals and plants repeatedly have observed more or less extensive modifications occurring as one-step mutations; in fact, Darwin himself discussed this phenomenon. The other flaw is that neo-Darwinism has only one agent to account for the mechanism of evolution, natural selection. This circumstance has two shortcomings; first, as natural selection operates at the ecological level or organization, it may account for the 'survival' of living organisms, but it ignores their 'creation'. For this purpose we need an epigenetic theory, concerned with the mechanisms through which plants and animals are reproduced. It is no coincidence that many of Darwin's macromutationist antagonists were embryologists , for very little insight in embryology suffices to demonstrate the falsification of the micromutation theory. The other shortcoming is that one mechanism is not enough, for there are two kinds of evolution, one is divergent (adaptive) and one is progressive. It so happens that natural selection may perfectly well account for progressive evolution, because it ensures the survival of dominant forms. It cannot, however, explain survival in general, for some organisms survive in isolation, thus avoiding the struggle for existence implied by natural selection.

Almost all the objections raised by Popper against neo-Darwinism are correct, and yet he does not draw the proper conclusion, namely, that the theory has been falsified on all points but one, namely, natural selection. This is indeed an evolutionary agent, even if it is less universal than implied by the Darwinian theory. As I have shown, it has exactly the same function as error elimination in Popper's theory on the growth of knowledge. In both cases the factor in question answers for progress, in the first case ensuring the survival of ever more dominant forms of living organisms, in the second for the establishment of ever better theories. I suggest that the analogy can be extended further because it is undoubtedly true that many bad theories may survive in isolation, and

furthermore, the history of science clearly shows that the advance in human knowledge is not outright gradual, rather, it occurs in great bonds, interrupted by periods of more modest advances.

Umeå, October 1986.

Filosofia ed evoluzione*

Commento a Michael Ruse: 'philosophy of biology' di Karl Popper

Sia Karl Popper che Michael Ruse sono dichiarati sostenitori della teoria dell'evoluzione attualmente dominante che va sotto il nome di 'neo - darwinismo'. Malgrado ciò le loro valutazioni della teoria differiscono notevolmente. Così, mentre Ruse considera che la teoria sia alla pari con altre teorie scientifiche . Popper ha dichiarato che «il darwinismo non è una teoria scientifica probabile ma è un programma di ricerca metafisico , una possibile struttura per teorie scientifiche verificabili». Le posizioni divergenti adottate dai due studiosi, biologi dilettanti e filosofi specialisti, sono di interesse considerevole per le persone interessate alla filosofia biologica. Il saggio presente è soprattutto un commento al lavoro in cui Ruse discute la filosofia biologica di Popper.

Popper afferma che l'evoluzione della vita sulla terra o della società umana è un processo storico unico (RUSE, 1977a, p. 639). Questo certamente è vero, ma esiste una fondamentale differenza tra i due processi riferiti da Popper. Così, se la storia tratta di singoli eventi che non si ripetono mai, l'evoluzione ha a che fare con l'acquisizione di proprietà ereditabili che sono riprodotte via via durante l'ontogenesi dei discendenti degli organismi in cui una innovazione sorge a suo tempo. Questa circostanza implica che gli evoluzionisti hanno una possibilità di saggiare le loro previsioni in un modo che è sconosciuto nelle scienze storiche. Una parte predominante degli eventi passati implicati nell'evoluzione ci resterà per sempre sconosciuta.

Un altro argomento a cui Popper si è applicato è l'adattamento-selezione. Per ogni osservatore della natura gli organismi viventi sono meravigliosamente 'adattati' a vivere nell'ambiente particolare in cui accade ad essi di vivere. Non riusciamo ad immaginare un organismo che continui ad esistere in un ambiente a cui non sia adattato, e se gli esseri viventi sono per necessità adattati al loro particolare mezzo, allora è difficile vedere come la selezione na-

turale possa essere resa responsabile della variazione nell'adattamento invocata dalla teoria dell'evoluzione. Si potrebbe certo suggerire che la selezione migliori l'adattamento, ma come la si potrebbe misurare? Se ogni organismo è adattato al suo ambiente particolare, è impossibile un confronto. Come Woodger, Popper si rende conto della debolezza di questo concetto. Prendete 'l'adattamento'. A prima vista la selezione naturale sembra spiegarlo e in un certo senso lo fa, ma è un modo poco scientifico. Dire che una specie ora vivente sia adattata al suo ambiente è, in effetti, quasi tautologia. In vero usiamo i termini 'adattamento' e 'selezione' in modo tale che possiamo dire che se le specie non fossero adattate sarebbero state eliminate dalla selezione naturale. Allo stesso modo se una specie è stata eliminata deve essere stata male adattata nell'ambiente (RUSE, 1977a, p. 646).

L'adattamento o 'fitness' è definito dagli evoluzionisti moderni come valore di sopravvivenza e può misurarsi dal successo reale nella sopravvivenza. È quasi impossibile saggiare una teoria vaga come questa (RUSE, 1977a, p. 646). Popper successivamente si occupa della gradualità dell'evoluzione, cioè della teoria della micromutazione. La gradualità è così, da un punto di vista logico, la predizione centrale della teoria (mi pare che sia la sua sola predizione). Tuttavia sinché i cambiamenti nella base genetica delle forme viventi sono graduali, essi sono per lo meno in linea di principio 'spiegati' dalla teoria; poiché la teoria predice l'accadere di piccoli cambiamenti, ciascuno dovuto a mutazione (RUSE, 1977a, p. 649). In realtà, ispirato dal lavoro di MACBETH (1971) Popper stesso ha giocato con l'idea delle macromutazioni, cioè con i 'mostri fortunati' di **Goldschmidt**. Pur-troppo egli suggerisce che le macromutazioni possano aver a che fare col comportamento più che con la morfologia. La teoria delle macromutazioni fu discussa da Ruse che fece la classica obiezione per dirne una pensiamo che questo mostro sia di una specie differente dei suoi genitori? Se non lo è , allora Popper ignora il grande problema evolutivo della speciazione. Se lo è, con chi va a riprodursi, poiché la specie dei suoi genitori è esclusa? (RUSE, 1977a, pp. 656, 657).

Secondo il mio punto di vista il lavoro di Popper dovrebbe aver convinto Ruse che se l'analogia tra evoluzione e avanzamento nella conoscenza deve essere completo, allora egli avrebbe dovuto abbracciare la teoria della macromutazione. Non sarebbe stato difficile dimostrare che l'analogia è esauriente nella misura in cui nel campo della conoscenza teorie obsolete possono sopravvivere in isolamento . Popper ha lui stesso indicato fenomeni tali come psicoanalisi, marxismo e astrologia (POPPER, 1972) .

Ho tentato qui di analizzare la critica che Ruse , ben noto aderente al neo-darwinismo , ha sollevato contro Popper , il quale pure afferma di credere nel valore di questa dottrina , anche se ne discute la validità come teoria scientifica. Così sulla base delle due asserzioni fondamentali del neo-darwinismo, micromutazione e selezione naturale, Popper arriva alla conclusione che in molti modi le prove empiriche disponibili corrispondono alle previsioni derivabili dalla teoria. Una ragione del diverso atteggiamento dei due autori è chiaramente che Ruse è molto più informato di Popper sulla letteratura di genetica di popolazioni, che egli frequentemente cita, forse meno criticamente di quanto ci si aspetterebbe.

In diverse occasioni ho mostrato che la teoria comunemente accettata ha due manchevolezze. La prima è che è una teoria di micromutazione. Da quando Darwin pubblicò la sua teoria, parecchi oppositori hanno asserito che molti cambiamenti evolutivi non possono essere stati l'esito di mutazoni con piccoli effetti. A sostegno dell'opposta teoria, secondo cui le macromutazioni sono ben più che una pura speculazione, è stato spesso citato il fatto che gli allevatori di animali e piante hanno ripetutamente osservato estese modifiche come effetto di mutazioni in un solo passo. L'altra manchevolezza è che il neo-darwinismo dispone soltanto di un agente per interpretare il meccanismo dell'evoluzione: la selezione naturale. Questa ha due limitazioni: prima, poiché essa opera al livello ecologico, può spiegare la 'sopravvivenza' degli organismi viventi, ma ignora la loro 'creazione'.

Per questo intento è necessaria una teoria epigenetica che si occupi del meccanismo con cui piante e animali si riproducono. Non è un caso che molti degli antagonisti macromutazionisti di Darwin fossero embriologi, poiché basta un po' di conoscenza embriologica per dimostrare l'incosistenza della teoria della micromutazione. L'altra limitazione è che un solo meccanismo non è sufficiente perché, come osservato da Lamarck, vi sono due tipi di evoluzione, uno è divergente (adattativo) e uno è progressivo. Così accade che la selezione naturale può perfettamente spiegare l'evoluzione progressiva, perché assicura la sopravvivenza delle forme dominanti. Non può tuttavia spiegare la sopravvivenza in generale, perché alcuni organismi sopravvivono in isolamento, evitando così la lotta per la vita implicita nella selezione naturale.

Quasi tutte le obiezioni sollevate da Popper contro il neo-darwinismo sono corrette, e tuttavia egli non trae le giuste conclusioni, cioè che la teoria è stata falsificata su tutti i punti tranne uno, la selezione naturale. Invero questo è un agente evolutivo anche se meno universale di quanto supposto nella

teoria di Darwin. Come ho mostrato essa ha esattamente la stessa funzione dell'eliminazione dell'errore nella teoria di Popper sulla crescita della conoscenza. In entrambi i casi il fattore in questione spiega il progresso, nel primo caso assicurando la sopravvivenza di forme vieppiù dominanti tra gli organismi viventi, nel secondo lo stabilirsi di teorie sempre migliori.
Suggerisco che l'analogia possa essere estesa ulteriormente perché è senza dubbio vero che molte cattive teorie possono sopravvivere in isolamento e inoltre la storia della scienza mostra in modo chiaro che l'avanzare nella conoscenza umana non è francamente graduale, piuttosto avviene con grandi salti, interrotti da periodi di più modesti sviluppi.

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